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LIMITS OF NEMATOSCELIS MEGALOPS IN THE NORTHWESTERN ATLANTIC IN RELATION TO GULF STREAM COLD CORE RINGS. I. HORIZONTAL AND VERTICAL DISTRIBUTIONS

by

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Limits of Nematoscelis megalops in the Northwestern Atlantic in relation to Gulf Stream cold core rings. I. Horizontal and vertical distributions

by Peter H. Wiebe[1] and Steven H. Boyd[1]

ABSTRACT

The hydrographic limit of the distribution of *Nematoscelis megalops* in the Northwestern Atlantic Ocean is usually marked by the abrupt changes in water properties across the Gulf Stream. There are, however, isolated but repeated occurrences of this species in the Sargasso Sea. In our study, individuals in the Sargasso Sea were expatriates from the Slope Water which had been transported to the collection site by Gulf Stream cold core rings with but two exceptions. The exceptional cases can be indirectly linked to the presence of rings.

Expatriated populations do not persist. Extinction in a ring appears to take place in one or two generations, and for *N. megalops* it is related to changes in hydrographic properties, and in particular, the vertical temperature structure. Both in the Slope Water and in the ring 50% or more of the population is found in a restricted temperature regime centered about 10°C. As a ring ages, the preferred temperature regime and *N. megalops* along with it move deeper into the water column. The physiological and biochemical data given by Boyd, Wiebe and Cox (1978) combined with data given here indicate that withdrawal from the surface results in progressive deterioration of the nutritional condition of the population, a cessation of growth, a drastic reduction in the number of males relative to females, reproductive incapacitation, and ultimate extinction. It is conceivable that a process similar to that occurring in rings is responsible for the maintenance of the Gulf Stream as a hydrographic limit in the distribution of *N. megalops*.

1. Introduction

The Gulf Stream in the Western North Atlantic demarcates a sharp physical oceanographic boundary. This boundary region is narrow (30 to 60 nm) and is characterized in the upper 1000 m by strong currents (2 to 5 knots) and by large horizontal changes in temperature (~ 10°C) and salinity (1 to 1½‰). The region is also one of high biological contrast with many of the Slope Water[2] organisms to the north of the boundary being distinct from species to the south in the Sargasso

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2. Slope Water is an oceanographically distinct band of water which lies between the Gulf Stream and the continental shelf. Relative to the adjacent water masses, it has intermediate salinity values 34 to 36‰ in the surface layers (upper 200 m) and relatively low temperatures in mid-depths (200 to 1000 m – 12 to 4°C) Wright, 1978.

Sea (Grice and Hart, 1962; Wiebe *et al.,* 1976a; Jahn and Backus, 1976). Although the horizontal gradients of physical properties across the Gulf Stream are large, a number of the zooplankton species on both sides of the boundary experience equally large changes either in their daily or seasonal vertical migrations or by virtue of having a wide vertical distribution. Thus, it is not clear precisely what factors make the Gulf Stream (and other Western boundary currents) such an effective barrier to the extension of biogeographic limits of oceanic species (Frost, 1969; Gilfillan, 1972, 1976).

The Gulf Stream is not a completely effective barrier, however, and expatriated populations are found both to the north and south. It now appears that one major way in which populations are mixed across the boundary is through the formation and decay of Gulf Stream rings (see Figure 1 in Parker (1971) for an illustration of ring formation). Rings with a warm core form to the north and transport typical inhabitants of the Sargasso Sea and Gulf Stream into the Slope Water (Haedrich, 1972). The reverse process results in organisms of Slope Water origin being isolated within a cold core ring and transported into the Sargasso Sea. As has been described by Wiebe *et al.* (1976a) and Jahn (1976), cold core rings are a significant contributor to the scale and frequency of regional biological variability in the Northern Sargasso Sea because of their widespread occurrence (10 to 15 at any one time) and their relatively long lifetimes (one to two years or longer—Richardson, 1976; Lai and Richardson, 1977). Once isolated, the organisms of Slope Water origin gradually disappear and are replaced by Sargasso Sea species in a process that appears to be associated with modification of the physical and chemical properties of the ring, especially the surface properties. As a likely consequence of the process of decay, Wiebe *et al.* (1976a) concluded that the decline of the Slope Water phytoplankton assemblages was more rapid than that of the zooplankton or midwater fish assemblages.

Because of the unique aspects of community translocation and subsequent decay associated with cold core rings, we have sought to use these large features as experimental sites where factors determining the biogeographic boundaries might be better elucidated. We have concentrated our study on a particular species of zooplankton, the euphausiid *Nematoscelis megalops* (Hansen). This species is classified by Brinton (1962), Mauchline and Fisher (1969) and Gopalakrishnan (1974) as an animal which inhabits transition regions between the tropical-subtropical and the subpolar waters in the Atlantic, Pacific, and Indian Oceans. Although records exist of substantial numbers of individuals occurring in the upwelling zone off Northwest Africa trailing off to occasional occurrences downstream (Baker, 1970; Gopalakrishnan, 1974; Moore, 1952), the species is primarily a high latitude transition zone form.

In the portion of the Northwest Atlantic Ocean which we have sampled (Fig. 1), *N. megalops* exhibits high fidelity (". . a measure of the restriction of a species to

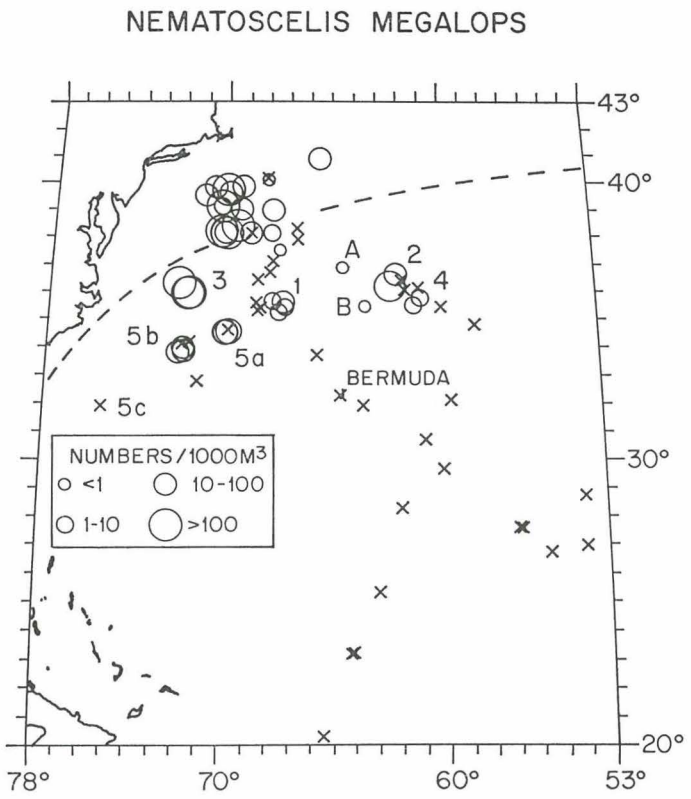


Figure 1. The horizontal distribution of *N. megalops* in the Northwestern Atlantic Ocean based on net collections in the upper 750-1000 m between 1972 and 1975. X's indicate where samples were taken and no individuals of *N. megalops* occurred. The dotted line indicates the mean axis of the Gulf Stream. Samples with *N. megalops* present which are clustered between 68W to 71W and 37N to 39N were all taken within the Slope Water. All other positive records to the south of the Gulf Stream axis were from samples in Gulf Stream rings except for records at locations A and B where in both instances a single individual was caught (see text for explanation of occurrences). Individual rings are numbered in order of the sequence in which they were sampled. Numbers 5a, b and c correspond to the location of ring D at successive sampling times (see Figure 3). The X's which appear to be within the area of ring 5b are actually negative records associated with collections made in the Sargasso Sea when the ring was at location 5a.

the community", Fager, 1963, p. 427) to the Slope Water community and the Gulf Stream marks its usual hydrographic limit. In this paper we present data on the horizontal and vertical distribution of *N. megalops* in our survey area and complementary data on size frequency and sex ratios. In Part II (Boyd, Wiebe and Cox, 1978), we present biochemical and physiological data on the nutritional condition of home range and expatriated populations of *N. megalops*. We seek to

Table 1. List of cruises and number of samples which were sorted and counted for *N. megalops*. All nets were made of 0.333 mm Nitex nylon gauze.

Cruise or area	Date	Number of Tows Day	Night	Type of net
Slope Water	June 1972	3		1 m diameter
Slope Water	August 1972	1		1 m diameter
Atlantis II 71	September 1972		18	1 m diameter
Chain 111	February 1973	1	5	1 m diameter and 70 cm Bongos
Knorr 35	November 1973		6	1 m diameter and 70 cm Bongos
Knorr 38	March 1973		21	1 m diameter
Atlantis II 85	October 1974†	3*	1*	1 × 1.4 m MOCNESS
Chain 125	August 1975	5*	6*	1 × 1.4 m MOCNESS
Knorr 53	November 1975	5*	5*	1 × 1.4 m MOCNESS
Oceanus 7	June 1976		1	1 m diameter

* Each tow provided 8 depth specific collections (see text for details).

† On two tows in the Sargasso Sea the maximum depth reached was 600 m during the day and 400 m at night.

explain the failure of *N. megalops* to persist in cold core rings and to relate this understanding to the factor responsible for the maintenance of its hydrographic limits.

2. Methods

The samples were collected on ten cruises to the Northwestern Atlantic Ocean (Table 1). On all cruises, an effort was made to sample to at least a depth of 750 m at each station. Collections were made with three types of net systems. A 1 m diameter ring net equipped with a flow meter was used on the early cruises either exclusively or as a supplement to 70 cm diameter opening/closing Bongo nets (McGowan and Brown, 1966). Generally three pairs of Bongo nets were towed simultaneously on the wire so as to sample the intervals 0-250 m, 250-500 m, and 500-750 m. On *Chain 111,* the Bongos were opened by messenger and closed by a preset flow meter triggered release; on *Knorr 35,* they were opened and closed by messengers with flow through each net monitored by a flow meter in the mouth of each net. Beginning on *Atlantis II* 85, a new multiple opening/closing net and environmental sensing system (MOCNESS-Wiebe *et al.,* 1976b) was used to gather depth specific collections. This is a nine net system in which the rectangular nets, each 1 m × 1.4 m at the mouth (effective area 1.0 m^2), are sequentially opened and closed upon command through conducting cable from the surface. The system also carries sensors to monitor temperature, depth, conductivity, flow through the net, and aspects of net function. Data from the sensors

were transmitted to the surface (for viewing in real time) as well as processing by a HP 2100 shipboard computer. The hauls with MOCNESS reported here were generally to 800 m with eight 100 m strata sampled as the system fished obliquely from the bottom of the haul to the surface. (The first net was always fished while paying the wire out in order to maintain a uniform drag throughout the tow and to prevent kiting when sampling of the strata was begun.) On occasion, the strategy of sampling with MOCNESS was altered so that hydrographic features observed while shooting the net to depth could be bracketed by the samples on hauling in. The mesh used on all the nets was 0.333 mm Nitex gauze. Except for tows with MOCNESS designed to elucidate day-night variations in vertical distribution at a station, most tows were made at night. The samples were preserved in 5-10% formalin buffered to a pH 8.0 with sodium borate.

Adult and adolescent *N. megalops* in the collections were generally sorted from the entire sample and counted. Occasionally when particularly large numbers occurred only an aliquot was counted. Also on early cruises, some samples were split immediately after collection and half used for biomass determinations by destructive techniques (dry weight and carbon). Thus only half of the sample was available for counting. Carapace lengths as measured along the midline from the anterior margin of the carapace behind the eye to the most posterior edge (Ruud, 1936) were determined for selected samples using either all individuals in a sample or a representative fraction.

In cases where stratified oblique hauls were made, the counts of *N. megalops* may be used either to show the vertical structure of the population, or they may be combined to form a composite tow for comparison with 1 m diameter net hauls. For this latter comparison, the catches for each stratum were standardized to numbers per 1000 m^3 and the average catch (per 1000 m^3) for the column was determined. Although we have not made a specific effort to intercalibrate the three nets, neither the total number of euphausiid species nor the total number of individuals caught by the nets showed an evident systematic bias.

3. Results

a. Horizontal distribution. The horizontal distribution of *N. megalops* in the Northwestern Atlantic (Fig. 1) is similar to that of other transition or arctic-boreal[3] species in this region. In the Slope Water it frequently occurs in large numbers and in our samples it has only been found south of the Gulf Stream in Gulf Stream cold core rings with but two exceptions. On *Knorr* cruise 38 (March 1974), an oblique 1 m net tow was taken in what hydrographically appeared to be waters of the Northern Sargasso Sea. A single gravid female *N. megalops* was collected. However, this sample (Fig. 1, location A) was later found to have been taken in

3. Zoogeographic terminology as defined by McGowan (1974, p. 12).

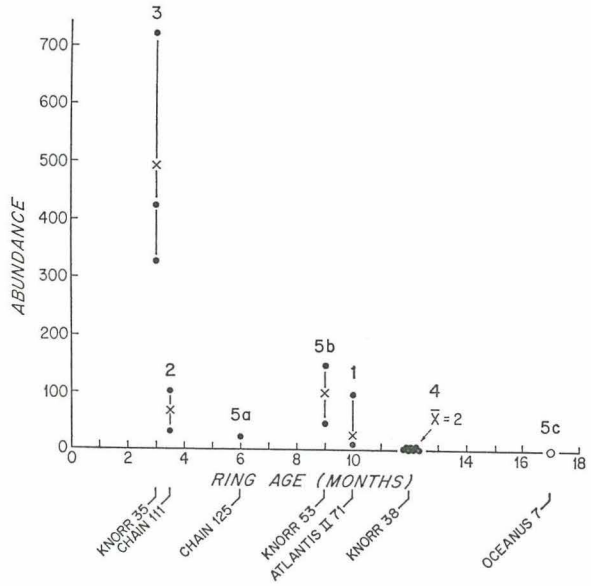


Figure 2. Abundance of *N. megalops* (#/1000 m³ in the upper 800 m) in cold core rings based on night collections only. The numbers above each data set correspond to the ring numbers given in Figure 1.

the wake of a cold core ring, the center of which was located by an aircraft expendable bathythermograph survey of the region (conducted by the U.S. Naval Oceanographic Office—NAVOCEANO) 30 days after the sample collection. At the time of the aircraft survey the center of this ring was less than 80 nm to the southwest of the collection site and since rings generally travel to the southwest it is reasonable to suggest that this individual may have been left behind in the wake of the ring as it moved through the Sargasso Sea. On the second leg of *Atlantis II* 71 in October 1972, another single individual was collected in the Sargasso Sea (Fig. 1, location B). No hydrographic data accompanied this tow, but, as in the first instance, a NAVOCEANO XBT survey of the region revealed a ring less than 60 nm to the southwest of the sample site within 25 days of the collection. Again it is reasonable to suggest that this individual was left by the passage of the ring. On a few occasions, *N. megalops* was not present in collections from the Slope Water. These have all been in or in the vicinity of warm core rings.

We have now sampled five cold core rings of different ages (3 to ~17 months). Most repeated day or night tows in a given ring provide estimates of abundance which are consistent within a factor of 2 to 4 of each other (Fig. 2). An exception is a tow (1 of 4) taken on *Atlantis II* 71 which caught ten times more individuals than any of the others. This large difference is probably due to real variations within the ring core since this particular tow was taken at the ring center where the coldest

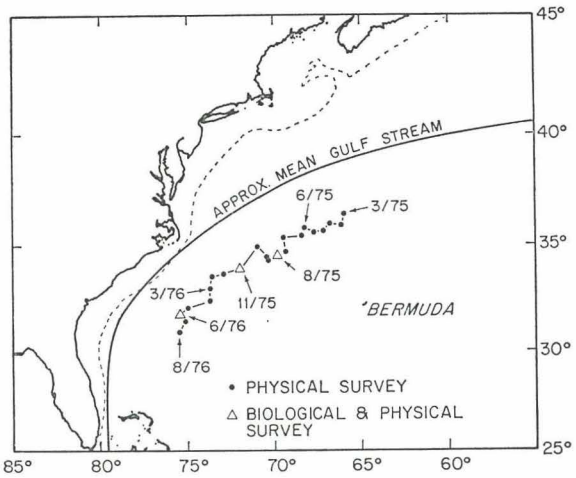


Figure 3. Position of the center of ring D versus time.

water temperatures were recorded. There is a general trend of decreasing abundance of *N. megalops* with increasing ring age culminating in the apparent absence of individuals in the 17 month old ring (Fig. 2). The four rings most responsible for the trend were only sampled once. In the one ring (designated ring D by NAVOCEANO) sampled more than once, however, abundance did not decrease monotonically (this will be discussed in greater detail by Boyd, Wiebe and Cox (1978). Difference in abundance levels between the two rings of 3 months of age are due, at least in part, to the season in which the rings were formed. There are large seasonal shifts in abundance of *N. megalops* in the Slope Water with largest numbers of individuals generally present in the late summer and early fall, and lowest numbers in midwinter and early spring. The 3 month old ring sampled on *Knorr 35* was formed at the beginning of September during a time of high abundance in the Slope Water while the other ring sampled on *Chain 111* was formed in late November when numbers in the Slope Water were substantially lower.

We sampled ring D at approximately 6 and 9 months (Figs. 3 and 4). It was previously surveyed by physical oceanographers at three, four, and five months of age and it was subsequently sampled by them at approximately 17 months (June, 1976). During this latter survey, a single but valuable oblique plankton tow was taken in the core of the ring (Fig. 3). Thus, although the spacing in time for the sequence of biological samples from ring D is not optimal, they do constitute the first set of biological time series samples from a cold core ring.

b. Vertical distribution. In our collections from the Slope Water, *N. megalops* typically lives in the upper 600 m with most individuals in the population occurring above 300 m both day and night (Fig. 5—see also Fig. 5, page 320 in Wiebe *et al.*,

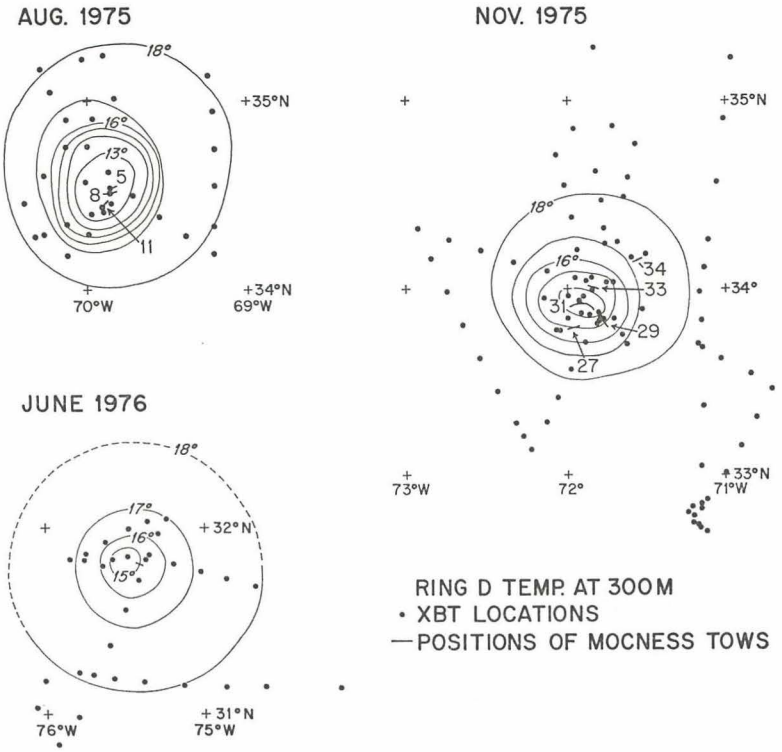


Figure 4. The 300 m temperature structure of ring D at the time of the biological surveys. Solid dots mark the position of 0-450 m XBT temperature profiles. Also plotted are the positions and lengths of MOCNESS tows in the ring area.

1976b). A similar vertical distribution pattern was observed in ring D at 6 months of age (August 1975) except that a larger fraction of the population was present below 300 m and individuals occurred down to 800 m. On the second cruise to ring D (November 1975), we found the vertical distribution had shifted significantly downward with the major portion of the population occurring below 300 m. At one point along the ring fringe (i.e., within the high velocity region of the Gulf Stream remnant encircling the Slope Water or core of the ring—tow #34, Figs. 4 and 5), four individuals were taken by the net which fished from 800 to 600 m. Since the ring was moving to the southwest at this time, these individuals were possibly in the process of being left behind in the wake region of the ring. If true, it lends credance to the suggestion that the individuals found in the Sargasso Sea on *Knorr 38* and *Atlantis II* 71 were outcasts from a nearby ring.

There were no *N. megalops* in the single night sample taken in the ring core on the third cruise to ring D (June 1976). Although this latter data is insufficient to make a definitive statement, we believe that the *N. megalops* population in ring D had completely died out at age 17 months (Fig. 2).

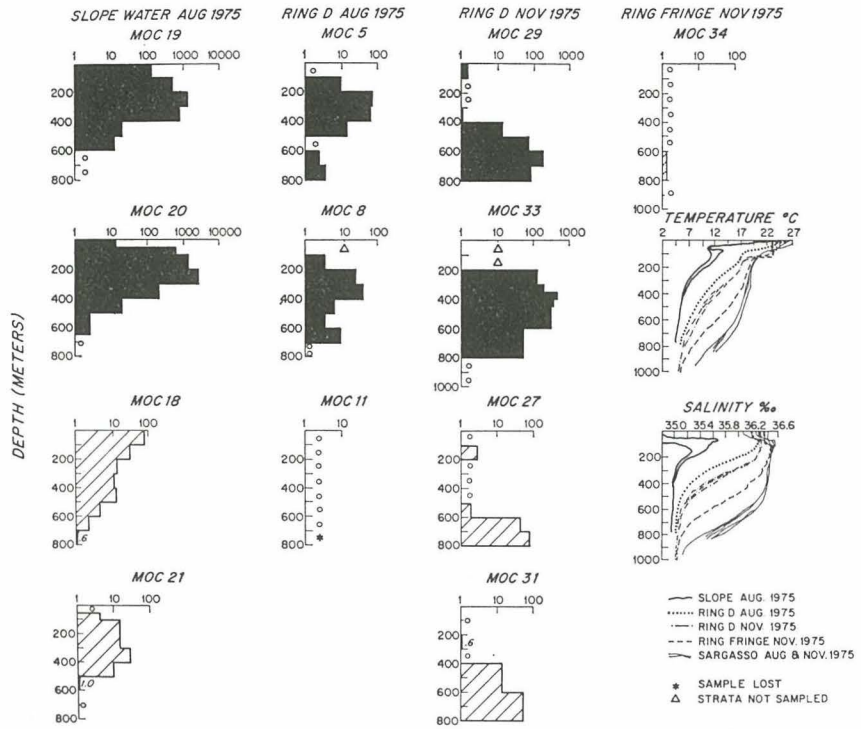


Figure 5. Vertical distribution of *N. megalops* in the Slope Water during August 1975 and in ring D during August and November 1975. Night samples are blacked; day samples are cross hatched. Also illustrated are the temperature and salinity profiles taken within each hydrographic area. (Abundance in #/1000 m³.)

A comparison of paired day and night tows in the Slope Water reveals that day catches are 1/10th to nearly 1/100th of the night catches. This difference is usually attributed to differential day/night avoidance of the nets. In ring D at 6 months, no individuals of *N. megalops* were taken (Fig. 5, tow #11) in the single day haul to 800 m. There is nothing unusual about the placement of this tow with respect to the core of the ring (Fig. 4) and no reason other than avoidance appears a likely cause of the result. Smaller differences were evident between day and night hauls in ring D at 9 months although the night catches were still larger than the day catches. In spite of the differences in catch between day and night, the basic pattern of vertical distribution at each station remains relatively unchanged (except in the case of ring D, tow #11). There is, therefore, no evidence for diel vertical migration in these collections of *N. megalops*. Except for tow #34 taken in the ring fringe, in the section which follows, we have used only data from the night collections to remove the possible bias due to differential day/night avoidance.

c. Relation of vertical distribution to temperature and salinity. Comparison of *N.*

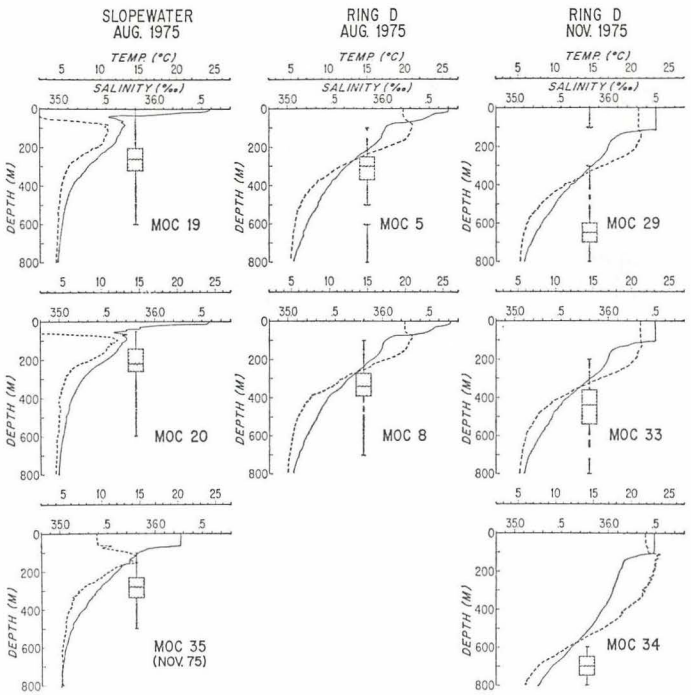
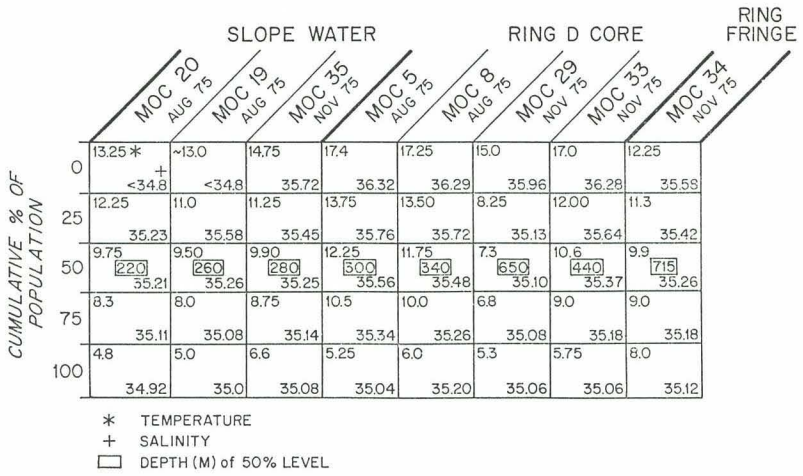


Figure 6. Comparison of the cumulative percentages of *N. megalops* in the Slope Water and ring D night MOCNESS tows with temperature and salinity. Individuals were cumulated from the surface down so that the top of the vertical lines represents the depth of first occurrences; the top, center, and bottom lines of the box represent the 25th, 50th, and 75th percentile of the population respectively; the bottom of the vertical line represents the last occurrence or the limit of sampling.

megalops's nighttime vertical distribution pattern with the simultaneously obtained temperature and salinity profiles indicates that the downward shift of 300 to 400 m in ring D was an attempt by the population to maintain itself in a well-defined temperature and salinity regime (Fig. 6 and Table 2). To make this comparison, we have calculated the cumulative percent of the population occurring to a particular depth in the same manner as Baker (1970). It is evident from Figure 6 that while the entire population has a remarkably wide vertical extent (~ 600 m), the central 50% of the population (i.e., between the 25th and 75th percentiles) lives in a rather narrow depth zone, generally less than 200 m, both in ring D and in the Slope Water.

The range of temperature and salinities experienced by the central 50% of the population in the Slope Water and ring D is also remarkably narrow (approximately 4°C and 0.5‰—Table 2). This portion of the Slope Water population both in August and November 1975 was collected from water with a midpoint temperature

Table 2. Values of temperature and salinity corresponding to the cumulative percentiles of *N. megalops* versus depth presented in Figure 6. The temperature and salinity values for the zero percentile in MOCNESS tow 19 are estimates based on information from another more finely stratified set of samples taken in the area but not reported in this paper.



of between 9.5 and 9.9°C and a salinity between 35.21‰ and 35.26‰. The same fraction of the ring D population of *N. megalops* at six months appears to have adopted a slightly higher temperature and salinity regime, but such a change is not evident in the ring D population at nine months. The variations in the temperatures and salinities between these eight sets of stratified oblique tows appear small relative to the large change in the depth distribution of the individuals as the ring decayed. Although data is presented in Boyd, Wiebe and Cox (1978) suggesting that the physiological condition of the population was deleteriously affected by environmental changes in the ring, our interpretation of these data is that individuals of *N. megalops* in ring D were actively adjusting their vertical distribution to stay within their preferred physical environment. It is noteworthy that in most of the vertical profiles the upper limit in vertical distribution of *N. megalops* coincides with the base of the seasonal thermocline. This thermocline deepens with ring age.

d. Size frequency and sex ratios of the Slope Water and ring populations. The effects of ring decay also appear evident in changes in the size frequency of the expatriated population relative to those observed in the home range population. *Nematoscelis megalops* carapace lengths in Figure 7 represent the pooled distributions of night collections (except MOC 34) made on *Chain 125* and *Knorr 53*. Carapace lengths for both the summer and fall sets of Slope Water collections show a bimodal size distribution indicating a dual age class structure. We assume these modes represent separate generations and have therefore labeled them GI and GII. In ring D at 6 months, contracted GI and GII modes appear to closely correspond with the

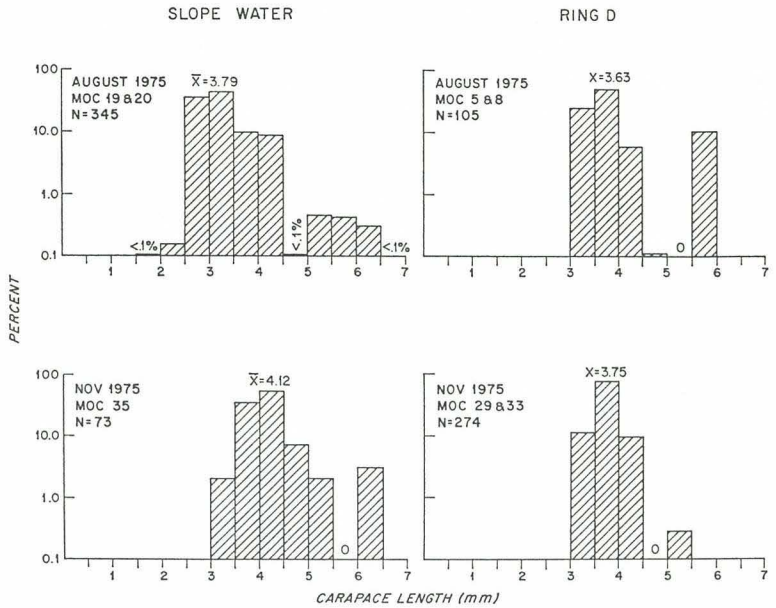


Figure 7. The size frequency distribution (in percent) of carapace lengths of *N. megalops* from the Slope Water and ring D MOCNESS tows made at night. *N* is the total number of carapace length measurements. The mean of the GII size class of individuals is given above each histogram. A log-scale was on the abcissa to permit both population modes to be observable in the face of the overwhelming numerical dominance of the GII size class.

same age classes in the Slope Water (Fig. 7) although ring individuals in the GII class are somewhat larger. In contrast, only a single size class (GII) was present in ring D at nine months (*Knorr 53*). If we assume that the same population was sampled on both occasions in the Slope Water, then growth measured in terms of mean carapace length increase was most rapid in the Slope Water GII size class averaging 0.9 mm in 90 days. Growth of the GII class in ring D over the same interval averaged 0.1 mm.

A pattern, frequently seen, of larger individuals in a population living deeper in the water column, is evident in our data (Fig. 8). This pattern is most apparent in the Slope Water profiles of size frequency versus depth, but is also quite noticeable in ring D at six months. The pattern is due to the absence of the larger individuals near the surface; smaller individuals generally occurred throughout the water column. With the loss of GI size class in ring D at nine months, the pattern of increasing average size with depth disappeared.

The ratio of females to males (♀ ÷ ♂) also provides a contrast between the Slope Water and the ring population. Our criterion for separating sexes is based only on the presence or absence of a petasma on the first pleopod. We have not attempted to examine females for the development of thelyca. In our samples

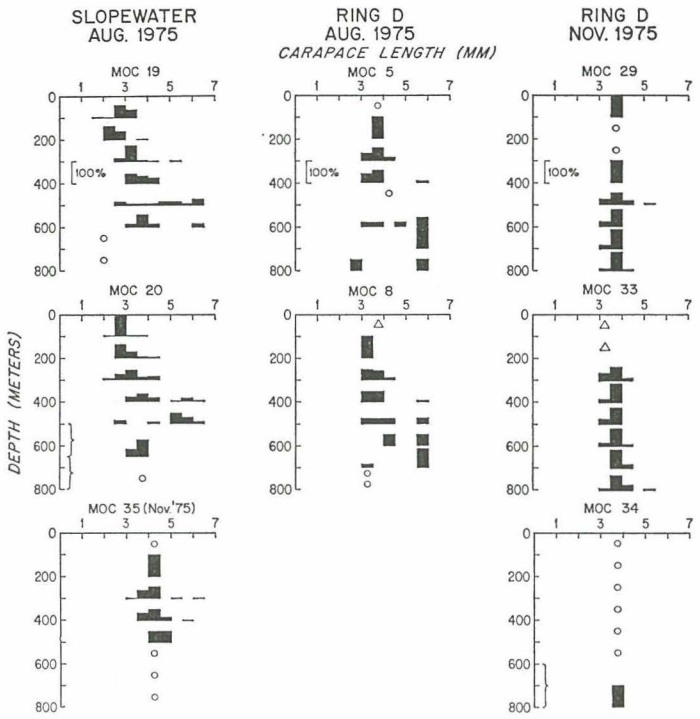


Figure 8. The size frequency distribution (in percent) of carapace lengths of *N. megalops* according to depth and area.

males with petasmas have carapace lengths between 3.0 and 5.0 mm while females may reach lengths up to 6.8 mm. All egg-bearing females observed were larger than the largest males.

Based on the entire set of Slope Water samples in different months between 1972 and 1975, there appears to be a seasonal cycle in the sex ratios. Males approximately equal the females during the late fall and winter months and are moderately to considerably outnumbered in late spring, summer, and early fall (Table 3). For some of the very large ratios during the period June to August, there is a distinct possibility that some of the many small individuals encountered (some < 3.0 mm in carapace length—Figures 7 and 9) were males which had not yet developed a petasma. However, this bias cannot account for all of the differences in the ratios, for if individuals less than 3.0 mm are excluded from consideration, the pattern remains evident.

The sex ratios of *N. megalops* in rings three months old are similar to the Slope Water ratios during the same season (i.e., November and February—Table 3). Generally fewer males are encountered in older rings. An exception to this is the 10-12 months old ring sampled in March 1974 in which a ratio of 0.8 was observed

Table 3. Sex ratios (♀ ÷ ♂) of *N. megalops* itemized according to season for collections from the Slope Water and cold core rings.

	1972				1973		1974		1975	
	June	Aug.	Sept.	Oct.	Feb.	Nov.	Mar.	Oct.	Aug.	Nov.
Slope Water Cruise	Slope Water	Slope Water	AII 71 Leg I	AII 71 Leg II	C111	K35	K38	AII 85	C125	K53
# Stations Pooled	3	1	2	1	3	1	4	1	2	1
# Individuals Examined†	69	18	80	31	71	78	20	80	349	72
R = ♀ ÷ ♂	5.6*	5.0	10.4	14.5	0.8	0.8	1.1	3.6*	51.0	1.5
Ring										
# Stations Pooled			4		2	2	3	1+	2	4
# Individuals Examined			46		92	167	8	2	105	1461
R = ♀ ÷ ♂			22.0		1.0	1.5	0.7	∞*	113.5	∞

+ Gulf Stream meander which was previously a ring.

* ♀ carrying eggs present.

† Note that the number of individuals examined is in some cases less than the total number of individuals present in the samples, i.e., sometimes aliquots were used to estimate the numbers of males and females. In addition, *R* was calculated after numbers were standardized to numbers/1000 m^3 and for MOCNESS tows after depth specific samples were pooled. Thus it is possible to have an *R* larger than the number of individuals examined.

in the total of eight individuals collected. The population of *N. megalops* in ring D exhibits the greatest contrast. Very few males were present in August (ring age—six months) and none were present in November (ring age—nine months) in spite of the fact that there were reasonable numbers of individuals in the collection (i.e., over 1400 inspected).

4. Discussion

Recent reviews of the horizontal distribution of *N. megalops* in the North Atlantic (Mauchline and Fisher, 1969; Gopalakrishnan, 1974) depict it as much less well-defined with respect to particular hydrographic regimes than in other parts of its oceanic distribution in which it has been reasonably well sampled (i.e., South Atlantic, and South Pacific Oceans). The distribution of the sibling species of *N. megalops, N. difficilis,* which occurs only in the North Pacific, is also portrayed as much more discrete. (We will refer to literature information about *N. difficilis* where possible, because these two species are so similar in morphology and have analogous geographic ranges and because there is a lack of data about the vertical distribution of *N. megalops* in the Pacific.)

In part, the wider range, especially in the western North Atlantic, stems from the isolated but repeated occurrences of *N. megalops* throughout the Sargasso Sea. In our collections, these occurrences are related directly or indirectly to cold core rings. We strongly suspect that Sargasso Sea records reported in the literature are due to rings as well. In the material Gopalakrishnan (1974, Fig. 8) examined, for example, there was a moderate catch of *N. megalops* southwest of Bermuda. The shallow temperature observations accompanying the collection (200 m BT) were interpreted by Backus *et al.* (1969) as indicating an oceanic front, however, it is equally plausible that isotherm shoaling was due to a cold core ring. The single *N. megalops* taken in one of a series of collections reported by Lewis (1954) from off Florida could also have been transported there by a ring. The area North of the Bahamas and east of Florida can aptly be turned a cold core ring "graveyard" because many of the rings which have been tracked appear to coalesce with the Gulf Stream and disappear in this area (Richardson, Strong, and Knauss, 1973; Lai and Richardson, 1977). It is our contention that in the Northwestern Atlantic the hydrographic limits of distribution of *N. megalops* are much more discrete than previously realized. In this area, it appears limited to waters originating to the north of the Gulf Stream and cannot survive in waters of the Sargasso Sea. In the discussion which follows, we will consider the reasons why this might be so.

The vertical distributions of *N. megalops* that we have observed in the Slope Water north of the Gulf Stream are quite similar to those presented by Waterman *et al.* (1939, Fig. 4A) derived from collections in the same area. Our Slope Water patterns are also consistent with those given by Baker (1970, Tables 1 and 2)

Table 4. A compilation of literature data on the temperature/salinity regime and the depth of occurrence of *N. megalops* and *N. difficilis*. Where enough information was given about the vertical distribution of the species, cumulative percentages versus depth were calculated for comparison with temperature and salinity data. In cases where physical and biological data were obtained from different sources, they are asterisked as follows: * = reference for biological data; ** = reference for physical data.

General Depth of occurrence	Temperature/salinity regime	Location	Comments	Author
		Norwegian Fjords		
>100-300 m	6.5-7.5°C; ~ 35‰ all year	Hardangerfjorden and Sognefjorden	Collections obtained with IKMT	Wiborg (1968)
>100 m	7.1-8.2°C; 34.5-34.9‰ all year	Byfjorden		
175-360 m	5.5-<8°C; 35.0-35.2‰ all year	Korsfjorden	Collections obtained with IKMT	*Jörgensen and Matthews (1975) **Matthews and Sands (1973)
		Mediterranean Sea		
>150 m	15-16°C; 39‰	Levant Sea	Collections obtained with IKMT only	*Wiebe and D'Abramo (1972)
>175 m	15-16°C; 38.4-38.8‰	Sidra Sea	Upper limit of vertical distribution at night sampled; total vertical distribution not known. Lower units of temperature and salinity cannot be below 12°C and 37.5‰.	**Miller, Tchernia, Charnock and McGill (1970)
>100 m	~15°C; 38.6-38.8‰	Ionian Sea		
>50 m	~14°C; 37.9-38.6‰	Tyrrhenian Sea		
>125 m	13-15°C; 37.0-38.1‰	Ligurian Sea		
>125 m	~13°C; 37.5-38‰	Balearic Sea		

	Cum % of Population							
	0	25	50	75	100	Location	Comments	Author
Depth (m):	410	460	490	580	630	Canary Islands	Collections obtained with N113 (1 m² and .333 mm mesh). Day	*Baker (1970) **Currie, Boden and Kampa (1969)
Temp. (°C):	12.0	11.6	11.3	10.4	9.9			
Salinity:	36.66	36.58	36.56	36.44	36.38			
Depth (m):	50	195	220	235	900	Canary Islands	Net as above. Night	*Baker (1970) **Currie, Boden and Kampa (1969)
Temp. (°C):	22.5	15.4	15.0	14.6	7.8			
Salinity:	36.46	36.14	36.08	36.02	35.21			
						Nematoscelis difficilis		
Depth (m):	0	100	160	230	500	California Current off San Diego, California	Collections with 1 m² net—(.333 mm mesh). Night. St. 100.35	Brinton (1967)
Temp. (°C):	15.5	10.2	9.4	8.9	6.3			
Salinity:	33.70	33.77	33.98	34.26	34.35			
Depth (m):	0	100	135	170	400	California Current off San Diego, California	Night. St. 100.60	Brinton (1967)
Temp. (°C):	15	11.3	9.5	9.3	6.7			
Salinity:	33.56	33.54	33.68	33.91	34.20			
Depth (m):	0	230	370	435	500	California Current off Monterey, California	Collections with 70 cm Bongo nets (.333 mm mesh). Night 27-28 Oct. 1970.	Youngbluth (unpublished)
Temp. (°C):	13.4	8.0	7.0	6.0	5.3			
Salinity:	33.39	34.09	34.21	34.19	34.17			
Depth (m):	0	130	185	220	400	California Current off Monterey, California	Night. 9-10 Nov. 1970	
Temp. (°C):	14.8	9.3	8.1	7.6	6.8			
Salinity:	33.17	33.81	33.90	33.96	34.17			
Depth (m):	0	50	90	160	400	California Current off Monterey, California	Night. 17-18 January 1971	
Temp. (°C):	11.9	10.5	9.9	9.2	6.6			
Salinity:	33.42	33.62	33.73	33.93	34.17			

for a population of *N. megalops* in the eastern Atlantic near the Canary Islands, and by Jorgensen and Matthews (1975, Fig. 12) for a population in Korsfjorden along the west coast of Norway. *Nematoscelis difficilis* exhibits a similar vertical distribution (Brinton, 1962, Fig. 63a,b; 1967, Figs. 17 and 18). In all of these areas, the bulk of the adolescent and adult population resides below the mixed layer and above 400 m both day and night, with the exception of the day collections of Baker (1970) where the day population resides between 400 and 600 m. The vertical distribution of *N. megalops* in the Western basin of the Mediterranean Sea appears in sharp contrast to that described above. Casanova (1970) reports that it is present between 300 and 1700 m during the day with a peak abundance at approximately 1000 m and that a fraction of the population migrates to within the surface waters (~100 m) at night.

Although Waterman *et al.* (1939), Brinton (1967) and Baker (1970) also interpret their data to imply that *N. megalops* (or *N. difficilis*) performs a diel vertical migration, most of the data, including ours, does not conclusively demonstrate that such is the case. As noted by these authors and apparent in this study, two aspects of its behavior confound this interpretation. First, *N. megalops* appears to exhibit strong differential day/night avoidance of sampling gear, with day catches being much smaller than night catches. Vision is thought to play an important role in this avoidance reaction (for example Brinton, 1967, p. 482), and there is the suggestion that the ability to avoid the net during the daylight may decrease with available light (and depth). Thus, even if there were no diel migration, differential avoidance of this type could result in decreased catches near the surface during the daylight and the appearance of migration. As reported above, in spite of fairly obvious differential avoidance in our collections, there is little evidence for pronounced shifts in *N. megalops*'s vertical distribution between day and night.

Second, the numbers of individuals taken in a suite of collections from a given area can be extremely variable, apparently because of swarming or patchiness. In the face of such variability, it is difficult to extract differences in vertical distribution patterns unless there are a number of pairs of day/night profiles. This problem may be significant in the studies of Waterman *et al.* (1939) and Baker (1970) as they acknowledge. We have also experienced large variations in closely spaced samples which we attribute to patchiness. This source of error does not, however, appear to be of sufficient magnitude to obscure recurring patterns in our data.

Contrasting sharply with the home range vertical distribution pattern which is typical for *N. megalops* in a number of geographic areas, is the shift downward with time for the population in ring D. As our results illustrate, the shift closely parallels the sinking of isotherms and isohalines that occur with ring decay, giving the appearance that individuals of *N. megalops* were actively maintaining them-

selves in a "preferred" temperature and/or salinity regime. The relative importance of temperature and salinity in eliciting this response is difficult to assess with our data alone. However, by using information given in previous studies, it is possible to infer that the adjustment in vertical structure in the ring was related to changes in temperature and not salinity. The data summarized in Table 4 are based on collections of *N. megalops* from three rather different North Atlantic hydrographic regimes (i.e., Norwegian fjords, Mediterranean Sea, and the Canary Current). The temperatures experienced by individuals in the populations from these areas are within the range of temperatures experienced by individuals in ring D or the Slope Water. In the fjords, temperatures where most individuals reside are low (5-<8°C), but within the limits of the deepest 25% of the Slope Water population. Throughout the Mediterranean Sea and off the Canary Islands, the temperatures are 2-4°C higher, but within the limits of the shallowest 25% of the Slope Water population. By comparison, the salinity regimes in which the North Atlantic populations live differ markedly. For the *N. megalops* in the Norwegian fjords, the salinities of their environment are fractionally lower (0.2-0.5‰) than those of the Slope Water. The reverse is true of the Mediterranean Sea population which is exposed to significantly higher salinities ranging between 37.5 and 39‰. Most individuals of *N. megalops* off the Canary Islands appear to live within the same salinity regime as the central portion of the Slope Water population during the day, while living in a fractionally higher (0.5-0.8‰) salinity regime at night. Thus, the various North Atlantic populations of *N. megalops* collectively experience salinities between 34.5 to 39.0‰. The point here is that although this species in adjusting its vertical distribution downward in ring D could be avoiding the higher than Slope Water salinities typical of the Sargasso Sea mixed layer, these salinities (~36.5‰) are considerably below those tolerated by the Mediterranean Sea segment of the North Atlantic population of this species.

Although the circumstantial evidence is strong that vertical temperature structure is a first order factor affecting the way *N. megalops* distributes itself vertically across the broad oceanic areas it inhabits, it is important to consider other factors which may be important. Gilfillan (1972, 1976) has recently discussed the relative importance of temperature and salinity to "other" factors in limiting the distribution of another species of euphausiid *Euphausia pacifica*. This species, endemic to the North Pacific, has a geographic range similar to *N. difficilis*. In a series of shipboard experiments along the California Current, Gilfillan (1972) demonstrated that *E. pacifica* could adjust to large changes in temperature and salinity of its environment. Of particular interest was the fact that the range of salinities tolerated (down to 24‰) without observable stress were considerably beyond those possible for it to encounter in the oceanic areas of its range. The upper limit in temperature tolerated (~15°C) without significant stress was, however, less than those possible for it to encounter along the southern and, in

the eastern Pacific, along the western parts of its range. In a second set of similarly executed experiments in the nearshore waters off British Columbia, Gilfillan (1976) found that *E. pacifica's* ability to withstand the stress of temperature or salinity extremes appeared to depend upon the source of the water which was experimentally manipulated. He concluded that "other" undefined water properties which related to the history of the water were responsible for the variations in susceptibility to stress. It is difficult for us, however, to see how "other" properties in this particular case can be interpreted as other than a second order effect. Without the primary stress introduced by the temperature and salinity extremes, "other" properties seemed to have a negligible effect.

There are additional factors such as light and oxygen which have been demonstrated to influence the pattern of zooplankton vertical distribution. Certainly for vertical migrators, light is of utmost importance. There are significant differences in the depth of penetration of isolume surfaces between the Slope Water and the Sargasso Sea (Lewis, 1954; Moore, 1952; Clarke and Backus, 1964). However, as discussed above, there is little conclusive evidence that *N. megalops* migrates to any great extent and to suggest that the difference in vertical distribution of the ring D and Slope Water populations was due to shifts in light levels ignores the fact that the diel changes in light are orders of magnitude larger than those between the two types of water and the species does not appear to respond to these. Also because of the large vertical extent of the population (>300 m), portions of the population were experiencing grossly different isolume levels (at least 4 orders of magnitude).

There is an additional and more compelling reason to believe that light does not appear to be a major factor influencing *N. megalops*'s vertical distribution during the period of this study. Secchi disc measurements made in ring D were similar in the two sampling periods (depths of approximately 33 m were obtained in the ring center on both occasions), thus indicating that the extinction coefficients of light in the upper 100 m were nearly equal. In contrast, incident radiation at the sea surface was 30% to 50% lower in the fall than in the summer due to seasonal changes in the inclination of the sun and a higher percentage of cloud cover. Given these conditions the depth of any given isolume shoaled and an organism following a particular isolume should also have shoaled if it were responding to light. Instead the depth distribution of *N. megalops* in the ring deepened.

Similarly, while very low concentration of oxygen (<0.2 ml/l) at mid-water depths has been strongly correlated with changes in the vertical distribution of some species of zooplankton (Banse, 1964; Bary, 1967; Longhurst, 1967), the minimum concentrations found in the Northwestern Atlantic (~3.0 ml/l) do not begin to approach the levels in which effects have been demonstrated.

Clearly we cannot demonstrate that there are no other factors exerting sufficient influence to cause *N. megalops* to change its vertical structure in ring D. If they

do exist, however, they must be correlated with vertical temperature structure.

In a number of respects, the pattern of withdrawal from the surface waters observed in the ring population of *N. megalops* is similar to larger scale geographical submergence of species associated with the submergence of water masses. For example, a close association between the planktonic polychaete worm *Poeobius meseres* and the Subarctic Water Mass in the North Pacific was described by McGowan (1960). Within the major portion of its home range, *P. meseres* was typically most abundant between 150 to 300 m, while in sampling south along the California Current the species was only caught in nets which were fished at progressively deeper depths (to greater than 1000 m south of 20N) in the submerging Subarctic Water. The series of vertical profiles presented by Omori (1967) clearly illustrates that the vertical and horizontal distribution of the copepod, *Calanus cristatus,* also appears strongly related to the distribution of Oyashio Water. In this case, submergence is initiated when the waters of the Kuroshio and Oyashio currents mix off the Island of Hokkaido (latitude 40-42N). South of this region along the eastern side of the Island of Honsyu, both the Oyashio Water and *C. cristatus* are found at successively deeper depths (down to 1900 m) whereas in the northern part of its range it lives near or in the surface waters. The most southerly published record of *C. cristatus* in this area is 28N.

Other features associated with the submergence are that *P. meseres* and *C. cristatus* both decrease in abundance with distance from their home range along the path of the submerging water mass. This parallels the pattern we generally see occurring with time in the ring *N. megalops* population. Evidence is also presented that indicates the submerged individuals, like the ring *N. megalops,* were living under unfavorable conditions. Omori (1967, p. 529) states that *C. cristatus* ". . . . were thin, almost transparent, and their stomachs were empty" and McGowan (1960) describes *P. meseres* in the southern extreme of its range, as although larger than average, frequently having degenerate viscera and missing gonads. The data presented by Boyd, Wiebe and Cox (1977) provide a picture of the ring populations being physiologically stressed by the environmental changes associated with ring decay. In contrast with Slope Water individuals, individuals of *N. megalops* in Ring D at age 9 months had significantly lower respiration rates, total body lipids and proteins (as indicated by reduced carbon and nitrogen).

5. Summary and conclusions

It is now possible for us to postulate that the hydrographic limit of distribution of *N. megalops* in the Northwestern Atlantic results from an interaction between the behavior of the species and temperature, and the effect that this interaction has on its nutritional status and reproductive capacity. Although we find individuals in this geographical region living within a rather broad range of temperatures and salinities, a significant fraction (50% or greater) of the adult population

is found in a much more restricted regime centered about 10°C. Our data suggest that in order for the population to grow and reproduce, the preferred regime must be close enough to the surface to permit adequate food concentrations and feeding opportunities. Even with the gradual warming, increasing salinity, and reduction in the standing stock of plankton biomass of the surface waters which is associated with the process of ring decay, there is no evidence that *N. megalops* acclimates to the change. Instead, this species remains bound to the preferred regime, and, as will be described by Boyd, Wiebe and Cox (1978), its physiological and biochemical condition declines. The season during which a ring is formed may be an important factor in determining whether successful recruitment to the initial expatriated population occurs. The *N. megalops* population may be able to produce young during the first three to perhaps six months of ring existence especially if ring formation took place during the Slope Water spawning period. However, in the later months growth and reproduction cease, largely, we believe, as a result of the deteriorated nutritional condition of the females and the drastic reduction of mature males. After one or two generations the expatriated population appears to become extinct.

We conceive of this process as taking place much more rapidly across the narrow faunal boundary constituted by the width of the Gulf Stream. Here in the space of 30 to 60 nm, the preferred regime undergoes an abrupt vertical change dropping from between 100 to 200 m in the Slope Water to below 800 m in the Sargasso Sea. Individuals transported across the Gulf Stream would probably have even less opportunity to acclimate to the radically different conditions of food size and concentration, species composition, as well as to the gross physical changes in temperature, salinity, etc., and it is possible that their demise could take place in a matter of days to weeks.

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18. SUPPLEMENTARY NOTES

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19. KEY WORDS *(Continue on reverse side if necessary and identify by block number)*

1. Cold core rings
2. Nematoscelis megalops
3. Horizontal-vertical distributions

20. ABSTRACT *(Continue on reverse side if necessary and identify by block number)*

The hydrographic limit of the distribution of Nematoscelis megalops in the Northwestern Atlantic Ocean is usually marked by the abrupt changes in water properties across the Gulf Stream. There are, however, isolated but repeated occurrences of this species in the Sargasso Sea. In our study, individuals in the Sargasso Sea were expatriates from the Slope Water which had been transported to the collection site by Gulf Stream cold core rings with but two exceptions. The exceptional cases can be indirectly linked to

(Cont. on back)

the presence of rings.

Expatriated populations do not persist. Extinction in a ring appears to take place in one or two generations, and for N. megalops it is related to changes in hydrographic properties, and in particular, the vertical temperature structure. Both in the Slope Water and in the ring 50% or more of the population if found in a restricted temperature regime centered about 10°C. As a ring ages, the preferred temperature regime and N. megalops along with it move deeper into the water column. The physiological and biochemical data given by Boyd, Wiebe and Cox (1978) combined with data given here indicate that withdrawal from the surface results in progressive deterioration of the nutritional condition of the population, a cessation of growth, a drastic reduction in the number of males relative to females, reproductive incapacitation, and ultimate extinction. It is conceivable that a process similar to that occurring in rings is responsible for maintenance of the Gulf Stream as a hydrographic limit in the distribution of N. megalops.

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WHOI-79-16

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II. Boyd, Steven H.

III. N00014-66-C-0241; NR 083-004

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